Review Article

Application of Combining Ability in Plant Breeding

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ABSTRACT

Combining ability is the ability of a genotype to transmit superior performance to its crosses. General combining ability is the average performance of genotype in a series of hybrid combinations and it measures additive gene action while specific combining ability is the performance of parents in specific crosses. Combining ability analysis helps in the identification of parents with high general combining ability (gca) effects and cross combinations with high specific combining effects (sca) for commercial exploitation of heterosis and isolation of pure lines among the progenies of the heterotic hybrids. Mating design refers to the procedure of producing the progenies in plant breeding. Plant breeders and geneticists use different form of mating designs and arrangements theoretically and practically for targeted purpose. Selection of good mating design is necessary for getting success in plant breeding. For production of different progenies and achievement of their objectives, plant breeders used different mating designs and arrangements. In all mating designs crossing is done in half sibs and full sib methods by taking individuals randomly. Selection of parental materials and good mating designs in conventional plant breeding are the keys to the successful plant breeding program. However, there are several factors affecting the choices of mating designs. Choice of mating designs depends upon several factors i.e. objective of study, time, space and other biological problems or limitations. In all mating designs, the individuals are taken randomly and crossed to produce progenies which are related to each other as half-sibs or full-sibs. A form of multivariate analysis or the analysis of variance can be adopted to estimate the components of variances. It provides easy and quick insight of the different form of mating designs and some statistical components for successful plant breeding. Generally, combining is playing a key role in estimation of genetic components and selection of suitable parents and hybrids in order to boost crop productivity. The knowledge of combining ability is very critical to determine the breeding procedure to improve the desirable traits. There is possibility to improve parents through selection, when the ratio of general combining ability to specific combining ability is greater than unity and if general combining ability to specific combining ability is less than unity, the breeding procedure is designed heterosis breeding to improve the desired traits.

Key words: Combining ability, General combining ability, Specific combining ability, Mating design.

INTRODUCTION

Combining ability is defined as the ability of an individual to transmit its desirable traits to its offspring when used in crossing program (Kambal and Webster, 1965). Combining ability studies, besides providing information on the nature of gene action also enable classification of selected parental material with respect to breeding behavior (formation of heterotic group). As a result, the concept of general combining ability and specific combining ability became useful for characterization of inbred lines in crosses (Hallauer and Miranda, 1988). Later developments in the characterization of genetic variance and type of gene action operative in crosses of inbred lines also often were interpreted relative to GCA and SCA of inbred lines. Different selection methods proposed for recurrent selection were also considered in the context of GCA and SCA and the type of gene action contributing to the heterosis expressed in crosses (Hallauer and Miranda, 1988). Selection may be practiced for additive gene effects with reasonable expectation for success in isolating the superior genotype and selection is less effective in isolating and fixing superior genotypes due to dominance and epistasis. The dominance gene action would favor the production of hybrids whereas the additive gene action indicates the standard selection procedures would be effective in bringing about advantageous changes to the character.

In another definition, combining ability is the parents' ability to combine among each other during hybridization process such that desirable genes or characters are transmitted to their progenies (Fasahat *et al.*, 2016). Combining ability is an estimation of the value of

genotypes on the basis of their offspring performance in some definite mating designs (Allard RW, 1999). Combining ability is a measure of gene action and helps in the evaluation of inbreds in terms of their genetic value and selection of suitable parents for hybridization. The concept of combining ability has become increasingly important in plant breeding. One of the concerns of plant breeders in the improvement of crops through hybridization is the choice of superior parents for yield and other desirable traits. Information on genetic systems controlling the inheritance of quantitative traits, particularly the nature and magnitude of gene action governing the inheritance of yield and related traits is necessary for a breeding strategy aimed at improving yield (Kang, 1997). Combining ability analysis helps in the identification of parents with high general combining ability (gca) effects and cross combinations with high specific combining effects (sca) for commercial exploitation of heterosis and isolation of pure lines among the progenies of the heterotic hybrids.

Breeding strategies based on selection of hybrids require expected level of heterosis as well as the specific combining ability. In breeding program, the breeders often face with the problem of selecting parents and crosses for the improvement of crop plants for high yielding and yield related traits. Combining ability analysis is one of the powerful tools available to estimate the combining ability effects and aids in selecting the desirable parents and crosses for the exploitation of heterosis. Combining ability is a useful measure of the suitability of genotypes as hybrid parents and as source material for the development of hybrid parents (Hallauer and Miranda, 1988). In addition to this, information on combining ability would be used to define the gene effects in the expression of quantitative traits (Goyal and Kumar, 1991). Combining ability is a useful method for comparing the performance of lines in hybrid combinations. This could be the average performance of a line in a series of crosses is known general combining ability whereas the performance of a specific cross known as specific combing ability (Sprague and Tatum, 1942).

Identification of the best performing lines (for commercial release) and lines which can be used as parents in future crosses are two principal objects considering in most crop breeding programs (Oakey H et al., 2006). The parental lines selection can be performed by particular mating designs such as line × tester, North Carolina (NC) designs and diallel. Through conducting such designs, the genetic influences of lines can be partitioned into additive and non-additive components (Topal A et al., 2004). General combining ability is defined as the average performance of a parent in hybrid combination and is recognized primarily as a measure of additive gene action whereas specific combining ability describes those cases in which certain hybrid combinations do relatively better or worse than what would be expected on the basis of the average performance of the parent and is regarded as an estimate of non-additive gene action such as dominance and epistasis (Hallauer and Miranda, 1988). The total genetic variance can be further subdivided into additive genetic variance, dominance genetic variance and epistatic genetic variance (Patel et al., 1992). Knowing the nature of gene effect based on combining ability information has a paramount importance for the breeder to design best

breeding strategy to select desirable parents or determine which breeding procedure will efficiently improve the performance of the traits of interest (Patel et al., 1992).

The relative importance of general combining ability and specific combining ability in a breeding system depends on the purpose of the breeding activity and the level of genetic improvement of parental lines involved in the crosses. General combining ability could be more important for estimating the potential of lines in germplasm development, whereas specific combining ability is more important when comparing performance of previously selected lines especially for yield and yield components (Sprague and Tatum, 1942). From the genetics point of view, general combining ability appears to be more important than specific combining ability in that the effect can be fixed through selection and specific combining ability can only exist in heterozygotes (Schertz and Johnson, 1984). Different mating systems have been employed to estimate the general combining ability and specific combining ability effects of various genotypes. It also serves to exploit heterosis and select desirable crosses for further evaluation. Heterosis refers to super performance of a hybrid compared to that of the parents (Kaya, 2005). The vigor of the hybrid is expressed in the F_i generation but subsequent inbreeding will result in the reduction of hybrid performance because of many of the loci that were heterozygous in the F_i will become homozygous.

The evidence obtained from research result showed that yield increment over the parental mean in the F_i generation reduces by 50% in the F_2 generation (Quinby and Karper, R.E, 1946). In hybrid focused on breeding programs, the knowledge of combining ability of the parents and the inheritance of the traits is vital. This information helps in optimizing the breeding approach, either selection when general combining ability (GCA) effects are important; inbreeding followed by cross breeding when specific combining ability (SCA) effects are principal or selection followed by hybridization if both are important; because general combining ability effects are attributed to mass of genes with additive effects and specific combining ability indicates predominance of genes with non-additive effects (Makanda et al., 2010). The nature and magnitude of gene action is an important factor in developing an effective hybrid breeding program. Combining ability analysis is an important tool to select best parents based on the information of the nature and magnitude of gene effects controlling quantitative traits. Combining ability analysis is, therefore, an important method to infer gene actions and it is frequently used by plant specially crop breeders to pick parents with a high magnitude of general combining ability (GCA) and hybrids with high magnitude specific combining ability (SCA) effects. In general, the general combining ability and specific combining ability all-encompassing effects are important determining factor of a hybrid's performance (Griffing, 1956). The identification of the best performing genotypes for cultivar release or use in future crosses as seed or pollen parental line are two major tasks in plant breeding programs. Parental line selection is based upon the evaluation of the combining ability of a genotype which can be determined in specific mating designs and evaluates a genotype based on the performance of its offsprings. The

particular mating designs allow the partitioning of the genetic influence into additive and non-additive components. The determination of the combining ability is of specific importance in the breeding of hybrid and synthetic cultivars for the evaluation of inbred lines and varietal components. Combining ability can also be used to evaluate cross combinations in self-pollinating crops. The objective/s of the review was to understand the role of combining ability in crop plant improvement.

CONCEPT OF COMBINING ABILITY

The concept of combining ability was first used by maize breeders in the USA in the 1930s to predict parental breeding value from their progenies. Combining ability in crosses is defined as the ability of parents to combine amongst each other during the process of fertilization to transmit superior performance and favourable genes to their progenies. Combining ability studies of germplasm facilitates its exploitation in breeding and the choice of suitable parents for superior hybrid combinations (Akinwale et al., 2014). The concept of combining ability is increasingly used nowadays both in plant breeding for selection of desirable parents. Information on relative importance of general combining ability variance and specific combining ability variance is of value in the development of efficient breeding programs in species which are amenable to commercial production of F_1 seed such as maize and sorghum and also for production of synthetic and composite varieties. Success on development of breeding populations and hybrid varieties is dependent on the availability of genetically complementary parents and the magnitude of heritability of economic traits (Hochholdinger and Hoecker, 2007). The combining ability of parents determines their potential value in breeding population and hybrid development to enhance yield and drought tolerance. Crosses between genetically unrelated parents result in vigorous F_1 hybrids and promising segregants.

In a classical breeding program, it is necessary to identify superior parents for hybridization and crosses to expand the genetic variability for selection of superior genotypes (Hallauer and Miranda, 1988). Knowledge of combining ability is essential for selection of suitable parents for hybridization and identification of promising hybrids in breeding program. Combining ability studies provide information on the genetic mechanisms controlling the inheritance of quantitative traits and enable the breeders to select suitable parents for further improvement or use in hybrid breeding for commercial purposes. Combining ability is necessary in identification of good parental lines in hybrid breeding programs (Kambal and Webster, 1965). Plant breeders can take advantage from such information on combining ability for developing high yielding lines and hybrids. Combining ability is used in understanding the nature of gene action involved in the expression of quantitative traits and to predict the performance of the progenies. Combining ability plays a significant role in crop improvement because it helps the breeder to determine the nature and magnitude of gene action involved in the inheritance traits. Combining ability is useful in selection of desirable parents for exploitation of hybrids and transgressive expressions and also to assess the ability of parents to generate potential hybrids with a reasonable level of stability.

Combining ability is useful for plant breeders to better understand genetic variance in inbred lines to identify desirable parents to use in commercial hybrid production. Plant breeders use results of research on combining ability to help select the best parents for development of hybrids or varieties (Hallauer and Miranda, 1988). Breeding method for the improvement of a crop depends primarily on the nature and magnitude of gene action involved in the expression of quantitative and qualitative traits. Combining ability analysis helps in the identification of parents with high general combining ability (GCA) effects and cross combinations with high specific combining ability (SCA) effects. Additive and non-additive gene actions in the parents estimated through combining ability analysis may be useful in determining the possibility for commercial exploitation of heterosis and isolation of pure lines among the progenies of the heterotic F_1. In addition, information on combining ability would be used to define the gene effects in the expression of quantitative traits (Goyal and Kumar, 1991).

Combining ability is an estimation of the value of genotypes on the basis of their offspring performance in some definite mating design. Generally, parents are selected based on their combining ability for the traits of interest. Parents that have high genetic variance components have high breeding value and impart large effects on their hybrids (Falconer and Mackay, 1996). Heritability and combining ability estimates are required for efficient identification of good parents (Falconer and Mackay, 1996). The success of any breeding program largely depends upon the choice of parents for hybridization. The ability of the parents to combine well depends upon the complex interaction among genes which cannot be judged by mere yield performance. Combining ability analysis is a powerful tool to estimate combining ability effects and helps in selecting desirable parents and crosses for exploitation of heterosis and involving them in production of desirable hybrids and segregates (Sarker et al., 2002; Rashid et al., 2007). Information on combining ability and heterosis is a valuable tool in determining superior parents and hybrid combinations in a hybrid breeding program.

General and Specific Combining Abilities

The concept of general and specific combining ability was given by Sprague and Tatum (1942). General combining ability (GCA) is the average contribution of inbred lines that the inbred makes to the hybrid performance in a series of hybrid combinations. The general combining ability of an inbred line is evaluated by crossing it with other inbred lines and comparing the overall performance of the single-cross progenies. General combining ability indicates the additive gene action affecting a genetic trait in such a fashion that each enhances the expression of the trait. The general combining ability variance provides estimate of additive genetic variance which is required for the estimation of narrow sense heritability (Griffing, 1956). General combining ability (GCA) is directly related to the breeding value of the parents and is associated with additive genetic effects, while specific combining ability (SCA) is associated with non-additive genetic effect predominantly contributed by dominance, or epistatic effects (Salgotra et al., 2009). Specific combining ability is

the contribution of an inbred line to hybrid performance in a cross with specified inbred lines, in relation to its contributions in crosses with an array of specified inbred lines. It indicates non-additive gene actions mainly a function of dominance. It is due to the deviation of heterozygote phenotype from the average of phenotypic values of the two homozygotes (Singh *et al.*, 1993).

Specific combining ability represents the non-fixable component of genetic variation and it is important to provide information on hybrid performance. The criterion for selection is by considering general combining ability effects (gca) of the parents. Since the parents with high mean values may not necessarily be able to transmit their superior traits into their progenies, it become necessary to access their compatibility to express their own high performance to the hybrids involving them. High specific combining ability effects resulting from crosses where both parents are good general combiners (good GCA × good GCA) may be ascribed to additive × additive gene action. The high specific combining ability effects also derived from crosses including good × poor general combiner parents may be attributed to favourable additive effects of the good general combiner parent and epistatic effects of poor general combiner, which fulfils the favourable plant attribute. High specific combining ability effects manifested by low × low crosses may be due to dominance × dominance type of non-allelic gene interaction producing over dominance thus being non-fixable.

General combing ability helps to evaluate the contribution of an inbred line to the hybrid performance, whereas specific combining ability is utilized to identify cross combination with superior performance (Sparague and Tatum, 1942). General combining ability is calculated for a specific trait as the positive or negative deviation of the mean offspring performance of a genotype from the grand mean of all offsprings included in the particular mating design. General combining ability is mainly caused by additive effects while specific combining ability is defined as the deviation of the performance of hybrid combinations from the performance expected on the basis of the general combining ability of the parental inbred lines. In hybrid breeding the particular combination of inbred lines out of many possible combinations is selected which exhibits the highest F_1 performance. Therefore, inbred lines are selected as parental lines based on the highest specific combining ability. Specific combining ability is determined by dominance, over-dominance and other non-additive genes effects.

A high general combing ability estimate indicates higher heritability and less environmental effects which implies higher achievement in selection. General combing ability effects represent the fixable and heritable component of genetic variance and have direct association with narrow sense heritability and homozygosity (Fasahat *et al.*, 2016). Selection is effective for achieving maximum genetic gain and it's due to additive effect of genes, whereas specific combining ability represents the non-fixable and non-heritable component of genetic variation. Specific combining ability is an indicative of heterosis and heterozygosity. Maximum genetic gain achieved through heterosis breeding rather than selection and was the result of dominance and epistasis (Fasahat *et al.*, 2016). Successful and sound breeding program depends on the correct understanding of gene action involved in determining the different characters. It is claimed that if the general combing ability variance is greater, it implies preponderance of additive gene action for the trait and if specific combining ability variance is greater, then the particular character is mostly under the control of non-additive gene action. If the ratio of general combining ability to specific combining ability variances was less than unity for all the traits indicating the predominant role of non-additive gene action and recommended to utilize non-additive variance through heterosis breeding (Machado *et al.*, 2002). As a general rule, GCA is the result of additive gene effects, while SCA is the result of deviations from the additive gene action caused by dominance and epistasis (Bernardo, 2014). In statistical terms, the GCA is the main effect while the SCA is an interaction effect (Bernardo, 2014). Kambal and Webster (1965) used the ratios of male GCA to the sum male GCA plus male GCA x location interaction and female GCA to the sum female GCA plus female GCA x location interaction to express stability of GCA of males and GCA of females over locations.

Mating Design

The term mating design refers to the system of mating used to develop progeny. In a sense, mating designs are used to estimate combining abilities of parental populations involved in making crosses and to determine the type of gene actions operating in the inheritance of the traits under investigation. In plant breeding, various mating designs and arrangements are used by breeders and geneticists to generate improved plants. Plant breeders need to quantify additive and non-additive components of genetic variance in order to determine appropriate selection methods to improve quantitative characteristics. There are a number of mating designs that can be used by plant breeders to estimate genetic parameters in a populations. The mating designs differ in the genetic material evaluated and which determines the extent to which additive, dominance and epistatic variances can be estimated. One of the concerns of plant breeders in improving crops through hybridization is the choice of superior parents for yield and other desirable traits and that combine well upon crossing. It is here that the concept of combining ability is important in plant breeding. It is especially useful in connection with testing procedures, in which it is desired to study and compare the performances of lines in hybrid combination.

Mating designs are used to estimate combining abilities of parental populations involved in making crosses and to determine the type of gene actions operating in the inheritance of the traits under investigation. Hence, combining ability studies, besides providing information of the nature of gene action, also enables classification of selected parental material with respect to breeding behavior. With a progress in biometrical genetics, several techniques are suggested for the estimation of combining ability. Griffing (1956) applied the concept of gca and sca in relation to diallel crossing system while Kempthorne (1957) proposed the concept of gca and sca in line × tester analysis. The selection of suitable parents and good mating designs are keys to the successful plant breeding schemes (Khan *et al.*, 2009). However, there are several factors affecting the choices of mating designs. The factors influencing the choice of mating design are (i) the type of

pollination (self- or cross-pollinated); (ii) the type of crossing to be used (artificial or natural); (iii) the type of pollen dissemination (wind or insect); (iv) the presence of a male-sterility system; (v) the purpose of the project (for breeding or genetic studies); and (vi) the size of the population required (Acquaah, 2012).

Before discussing the mating designs, it is very important to understand the genetic assumptions (Hill, 2010) : (a) Diploid behaviour at meiosis; this assumption applies to all designs, but it doesn't preclude the investigation of polyploidy species provided they behave as functional diploids, with disomic inheritance. (b) Uncorrelated genes distribution. The genes controlling the character should be independently distributed among the parents. (c) Absence of non-allelic interactions. In the triple test and diallel crosses epistasis can be detected and its effects including in prediction. (d) No multiple alleles at those loci controlling the character. (e) Absence of reciprocal differences. Again this assumption can be tested in several designs and appropriate measure taken. (f) Ideally the diallel cross should be restricted to crosses among homozygous lines. Heterozygous can be catered for, but it complicated the interpretation of the results. (g) Absence of genotype-environment interaction.Their presence merely emphasizes the need for wide scale testing of material in order to determine the extent of such interaction. The mating designs have four main importance, (1) to provide information on the genetic control of the character under investigation; (2) to generate a breeding population to be used as a basis for the selection and development of potential varieties; (3) to provide estimates of genetic gain and (4) to provide information for evaluating the parents used in the breeding program (Acquaah, 2012). In making various crosses breeders have interests in discovering the answer to the following questions: how significant is genetic variation? How much of the variation is heritable? And what types of gene affecting that significance? However, these are answered by comparing the variances of the segregating and the non-segregating generations (Kearsey and Pooni, 2003). Another interest of the breeder is identifying plants with superior genotypes as judged by the performance of their progeny. Suitable inbreds or lines are selected based on combining ability effects with better mean performance. Combining ability depends on the gene action controlling the trait to be improved. General combining ability (GCA) is the average performance of a line in hybrid combinations and is due to additive genes action.

The estimation of GCA for a particular line depends upon the mating design, but essentially, it is the deviation of its progeny mean from the mean of all lines included in the trial (Acquaah, 2012). Thus, theoretically, differences between maternal groups measure variation in their general combining ability. Specific combining ability (SCA) refers to combinations or crosses that do relatively better or worse than would be expected based on the average performance of the lines involved, it is therefore due to non-additive gene action (Acquaah, 2012). The information regarding the estimates of combining ability and genes actions is vital for a successful plant breeding (Panhwar *et al.*, 2008). Plant breeding experiments use two types of design, (1) mating and (2) experimental design which should march with its statistical components analysis and interpretation.

Therefore, this review provides the different form of mating designs and some statistical components for successful plant breeding; these will serve as reference to the scientists and students in the domain of plant breeding and genetics.

Major Mating Designs in Plant Breeding and Genetics

Mating design refers to the procedure of producing the progenies in plant breeding. Plant breeders and geneticists, theoretically and practically use different form of mating designs and arrangements for targeted purpose. However, the choice of a mating design for estimating genetic variances should be dictated by the objectives of the study, time, space, cost and other biological limitations. Thus, several studies (Griffing, 1956; Acquaah, 2012) described and contrasted different mating designs and six types of mating designs have been described so far: bi-parental progenies (BIP), polycross, topcross, North Carolina (I, III, III), Diallels (I, II, III, IV) and Line x tester design. In all mating designs, the individuals are taken randomly and crossed to produce progenies which are related to each other as half-sibs or full-sibs. A form of multivariate analysis or the analysis of variance can be adopted to estimate the components of variances.

Bi-Parental Mating

The bi-parental design is called paired crossing design and is reported to be the simplest mating design (Mather and Jinks, 1982). In this design, the breeder selects a large number of plants (n) at random and cross them in pairs to produce 1/2n full-sib families (Acquaah, 2012). Their progeny are tested and the observed variation partitioned by straightforward analysis of variance into between and within families (Hill, 2010). Statistically, if r plants per progenies family are evaluated, the variation within (w) and between (b) families may be analyzed as follows: The simplicity of this design is counterbalanced by its inability to yield sufficient information to estimate all parameters required by the model (Acquaah, 2012).

This is because the progeny from this design are either full sibs or unrelated; no other relationship exists among them. The estimates of the parameters can only be obtained either by simplifying assumptions, or if extra statistics become available (Hill, 2010). If dominance is assumed to be absent (VD=0), and there is no common environment (VEW=0), that is individuals from the same family do not share the same environment. Consequently, if these assumptions are unjustified, it will lead to an overestimate of the genetic component relative to the environmental component. These difficulties can be circumvented to a limited extent in practice.

In BIP design, extra statistic can be generated if information on the parents is available, or by inclusion of the selfed progenies of parents (Kearsey, 1970). However, in practice both options are of limited value; because of the problems posed by presence of genotypes-environment interaction when considering parent-offspring correlation, and introduction of additional parameters. The BIP design, though simple to execute, has obvious limitations. Because no constraints have been imposed upon the mating there is a lack of relatedness among the resultant progeny. Consequently, unjustifiable assumptions many be required if estimated of the most important genetic and

environmental components are to be obtained (Hill, 2010). The most limitation of this design is its inability to provide the needed information to estimate all the parameters required by the model. The progeny from the design comprise full sibs or unrelated individuals. There is no further relatedness among individuals in the progeny. The breeder must make unjustifiable assumptions in order to estimate the genetic and environmental variance.

Polycross

This design is for intermating a group of cultivars by natural crossing in isolated block. Term polycross was coined by Tysdal, Kiesselbach and Westover to indicate progeny from seed of a line that was subject to outcrossing with other selected lines growing in the same nursery (Hill, 2010). It is most suited to species that are obligate cross-pollinaters (e.g., forage grasses and legumes, sugarcane, sweet potato), but especially to those that can be vegetatively propagated crops such as sugarcane, cassava and sweet potato (Acquaah, 2012). The design provides equal opportunity for each and every clone or parent to naturally cross with each other in the block such that self-pollination is prevented (Saladaga, 1989). However, to achieve this objective, a proper design in the polycross block is critical. It is critical that the entries be equally represented and randomly arranged in the crossing block (Falconer and Mackay, 1996).

The Latin square experimental design was suggested to be used as the most appropriate design to ensure all entries have equal chance of random intermating with each other in the polycross nursery (Morgan and Chakravarti, I.M, 1988). Nevertheless, when the entries number is more than 10, the completely randomized block design may be used (Acquaah, 2012). In both cases, about 20-30 replications are included in the crossing block. The ideal requirements are hard to meet in practice because of several problems, placing the system in jeopardy of deviating from random mating. If all the entries do not flower together, mating will not be random. To avoid this, the breeder may plant late flowering entries earlier. The design is used in breeding to produce synthetic cultivars, recombining selected entries of families in recurrent selection breeding programs, or for evaluating the GCA of the parent genotypes (Acquaah, 2012). The general combining abilities estimated are basically for maternal parents and the variations measured in a progeny can be partitioned into within and between maternal parents (Falconer and Mackay, 1996) and consequently, general combining ability helps in estimating heritability.

The mean performance of the progenies of any female parent in the polycross is used to determine the variance components and consequently the general combining ability (GCA). The heritability calculated provides decision guidance for usefulness of polycross in breeding programme (Saladaga, 1989). However, since the parents are of different origin and the crop is sensitive to environmental changes, the performance of the parental lines and their progenies such as flowering is likely to be affected (Morgan and Chakravarti, I.M, 1988). In addition, the differences in performance of progeny clones could arise from variations in heritability of trait measured (Gorz and Haskins, 1971). Consequently these could lead to inaccurate estimates of GCA; hence heritability determined

needs to be treated with caution. It is convenient to use polycross design in cross-pollinated species when evaluating a large number of genotypes (Gorz and Haskins, 1971). The selection is then applied based on half-sib progeny means. However, polycross design has a number of limitation such as random mating, insufficient statistics to estimate all the parameters, the component of variance are only estimated from the maternal half sibs; information about the males is lost, no control over the pollen source; expected genetic gains are reduced by half, the nonrandomness of mating (due to lack of synchronisation of flowering, unequal pollen production and position effects in the crossing block). The polycross is ideally suited for identifying mother plants with superior genotypes from the performance of their progeny general combining ability (Hill, 2010).

Top cross design

Topcross refers to a mating between a selection, line, clone and a common pollen parent which may be a variety, inbred line or single cross. The selected plants are crossed with a common tester(s) of known performance, generally in open pollination. The design was proposed by Jenkins and Brunsen in 1932 for testing inbred lines of maize in cross-bred combinations and later renamed topcross by Tysdal and Grandall (Hill, 2010). The tester parent should have well known genetic background; either narrow- or broad-based testers (Aly et al., 2013). The purpose of using top is to increase the chance of obtaining a desirable gene or genes from exotic or difficult materials. Exotic refers to lines from other countries which are generally poorly adapted to local conditions. Difficult material refers to varieties or lines which are tall, poor combiners, or dominant susceptibles, etc. i.e. lines which have given poor results (progeny) from single crosses in previous crossing cycles.

In making top crosses, only single cross F_1's are utilized because they are uniform. The top cross F_1's will be segregating and it is impossible to identify superior plants at crossing; therefore, they are not used. The F_1's are selected for desirable agronomic characteristics or for desirable parentage. Topcross has been fairly widely used for preliminary evaluation of combining ability of new inbred lines (Mosa, 2010). The possible numbers of crosses are n x 1, given n number of inbreds. Topcross progenies yield only GCA information, not SCA. It is a simple and efficient system of screening inbred lines for combining ability before pairing inbreds in single-cross yield trials. This design is probably the simplest model of mating design that can provide preliminary rapid screening of genetic stocks as it involves the lowest crossing load and simple statistical analysis (Mosa, 2010). The design has two shortfalls. First, a single tester variety may not offer wide genetic background for testing the inbred stocks. Secondly, the numbers of crosses become large if the test inbreds are many.

North Carolina

North Carolina design was developed after using long time diallel. However, the later require much labour. Therefore, in order to obtain more information about combining ability but without much labour comparing to full diallel, Comstock and Robinson in 1952, introduced

the North Carolina designs I, II, and III. North Carolina Design I: It is a very popular multipurpose design for both theoretical and practical plant breeding applications (Acquaah, 2012). It is commonly used to estimate additive and dominance variances as well as for the evaluation of full- and halfsib recurrent selection. It requires sufficient seed for replicated evaluation trials, and hence is not of practical application in breeding species that are not capable of producing large amounts of seed. It is applicable to both self- and cross-pollinated species that meet this criterion. NC Design I is a hierarchical design with non-common parents nested in common parents (Acquaah, 2012). The progenies include both full-sibs and half-sibs. Each set of families with the same father in common constitutes a half sib family group and a set of families with both parents in common constitutes a full-sib family (Kearsey and Pooni, 1996).

The NCI has advantage over biparental and polycross designs, because it gives three statistics compared with only two in the polycross and biparental (Kearsey and Pooni, 1996). Like the polycross, the main advantage of design I is its ability to supply a test of significance for the additive genetic variance. Also, NCI has been used successfully to tree breeding where mass collection of pollen from common parents possess no practical problems (Hill, 2010). Further, the design is applicable to both self- and cross-pollinated crops. However, this design is most widely used in animal studies. In plants, it has been extensively used in maize breeding for estimating genetic variances (Acquaah, 2012). North Carolina Design II : In this design, each member of a group of parents used as males is mated to each member of another group of parents used as females. It is used to evaluate inbred lines for combining ability. The design is most adapted to plants that have multiple flowers so that each plant can be used repeatedly as both male and female. Blocking is used in this design to allow all mating involving a single group of males to a single group of females to be kept intact as a unit (Acquaah, 2012). The design is essentially a two-way ANOVA in which the variation may be partitioned into difference between males (m) and females (f) and their interaction.

This design also allows the breeder to measure not only GCA but also SCA (Acquaah, 2012). However, the NCII is not providing test of epistasis or G X E interaction (Kearsey and Pooni, 1996). In North Carolina II, every progeny family has half sib relationships through both common male and common female. This is accomplished by systematic crossing program in which n_1 male and n_2 female are mated in all possible combinations to give n_1n_2 progeny families. It is therefore a rectangular mating design, unless $n_1=n_2$. Reciprocal crosses may be carried out to analyze maternal effects (Hill, 2010). North Carolina Design III: In this design, a random sample of F_2 plants is backcrossed to the two inbred lines from which the F_2 was descended. It is considered the most powerful of all the three NC designs. However, it was made more powerful by the modifications made by Kearsey and Jinks that add a third tester not just the two inbreds (Acquaah, 2012). The two parental lines act as testers against which F_2 are assessed. The parents being progenitors of the F_2, are very special testers because F_2 is segregating at all loci for which the testers differ but for no other loci (Kearsey and Pooni,

1996). The F_2 population is reference population for mating NCIII (Hallauer *et al*., 2010).

The modification is called the triple test cross and is capable of testing non-allelic (epistatic) interactions, which the other designs cannot, and also capable of estimating additive and dominance variance (Acquaah, 2012). According to Hill, 2010, it is also called triple test cross because of inclusion of the third tester. This inclusion increase the power of this design considerably, because it provides a sensitive and unambiguous test for non-allelic interactions, a capability which none of the designs described so far, not even design 3 in its original form possess. Moreover, both in its original and extended form design 3 has a general utility for investigating any population, irrespective of gene frequency or mating system (Hill, 2010). In triple test cross a random sample of n individuals from the population under investigation is crossed to the same three testers, L_1, L_2 and L_3 to give 3n progeny families. The analysis of this design may be divided into two parts, the first part supplies a test for epistasis, and the second assesses the significance, and provides estimates of the additive and dominance components of variation. The NCIII is a special case of NCII, therefore the ANOVA is similar to that of the NCII although it differs in one special feature; the two testers are not a random sample from any population but are two very particular lines, the progenitor of the F_2.

Diallel design

The diallel is the most used and abused of all mating designs in obtaining various genetic information (Hallauer *et al*., 2010). Much of its abuse could probably be due to the presence of two models for diallel analysis; random and fixed models (Griffing, 1956). A random model involves parents that are random members of a random mating population. A random model is useful for estimating GCA and SCA variances. In contrast, when parents are considered fixed effects, the aim is to measure the GCA effect for each parent and the SCA effect for each pair of parents. These effects only apply to the set of parents in the diallel. It is also widely used for developing breeding populations for recurrent selection (Acquaah, 2012). In addition, Johnson and King (1998), reported that diallel mating designs are deployed to provide the maximum opportunity to manage co-ancestry in breeding population and maximize selection differential. In diallel mating, the parental lines cross in all possible combinations (both direct as well as reciprocal crosses) to recognize parents as best or poor general combiners by general and the specific cross combinations by SCA.

A complete diallel mating design is one that allows the parents to be crossed in all possible combinations (Schlegel, 2010), including selfs and reciprocals. This is the kind of mating scheme required to achieve Hardy–Weinberg equilibrium in a population (Acquaah, 2012). Complete diallel cross designs entail the occurrences of equal numbers of each of the different crosses among p inbred lines. When p, is large, or reciprocal crosses are analogous to direct crosses it becomes impractical to conduct an experiment using a complete diallel cross design. In such circumstances, partial diallel cross designs (a subset of crosses) can be used. The most frequently used methods in the diallel analysis are Griffing's (1956) diallel

procedures. Griffing (1956) suggested four different diallel methods for use in plants: 1) Method 1 (full diallel): parents, F_1 and reciprocals, 2) Method 2 (half diallel): parents and F_1's, 3) Method 3: F_1's and reciprocals, 4) Method 4: F_1's. The number of progenies generated from each method are different, the number of progeny families (pf) for methods 1 through 4 are: $pf = n^2$, $pf = 1/2n (n + 1)$, $pf = n(n-1)$, and $pf = 1/2n(n-1)$, respectively (Acquaah, 2012). These four methods have been widely used to study the patterns of inheritance of different traits in many crops.

This mating design provides information on GCA and SCA (Griffing, 1956). However, the fixed model of method 3 or 4 is the most appropriate for obtaining unbiased estimates of combining abilities and gene action (Shattuck et al., 1993). This method is most suitable when there are no genotypic reciprocal effects (Griffing, 1956). The most of the problems arising with diallel crosses are essentially due to experimental design such that analysis of data is complex (Johnson and King, 1998). A relatively larger GCA/SCA variance ratio demonstrates importance of additive genetic effects and a lower ratio indicates predominance of dominance and/or epistatic gene effects. GCA and SCA effects for individual lines are calculated only when the overall analysis shows that mean squares for GCA and SCA are significant.

Line × Tester Design

Line x tester mating design was first proposed by Kempthorne in 1957 cited by Sharma (2006). This design involves hybridization between lines (f) and wide based testers in one to one fashion generating f x m = fm hybrids (Sharma, 2006). It is the simplest mating design that provides both full-sibs and half-sibs simultaneously as opposed to topcross which provides only half-sibs. It provides SCA of each cross, and it is not providing GCA of lines only but of the testers also, as liner and tester both are different sets of genotypes (Sharma, 2006). It is therefore most suitable for animal experiment (Sharma, 2006). In addition, it is used in estimating various types of gene actions important in the expression of quantitative traits (Rashid et al., 2007). Line x tester is basically an extension of top cross design in the sense that instead of one tester as used in top cross, more than ones testers are used under L x T mating design. This design involves hybridization between lines (f) and wide based testers (m) in one-to-one fashion generating f x m = fm hybrids (Sharma, 2006). Line × tester analysis is one of the most powerful tools for predicting the general combining ability (GCA) of parents and selecting of suitable parents and crosses with high specific combining ability (SCA) (Rashid et al., 2007).

The line x tester mating design for combining ability suggested by Kempthorne (1957) is an appropriate method to identify superior parents and hybrids based on GCA and SCA respectively. It is also helpful for estimating the nature and magnitude of gene action controlling quantitative traits. Line × tester is useful in deciding the relative ability of female and male lines to produce desirable hybrid combinations. It provides information on gene effects in controlling inheritance of traits of interest and helps in selecting the parents to be included in cultivar improvement or hybridization programs. It is the best way to test the value of a germplasm and identify the best parents to produce superior hybrids (Mindaye et al., 2016). The line × tester is the most widely used mating design for hybrid development. Line × tester mating design involves lines (l) and testers (t) in the generation of hybrids.

Conclusion

One of the concerns of plant breeders in the improvement of crops through hybridization is the choice of superior parents for yield and other desirable traits. Combining ability is the cultivars or parents ability to combine among each other during hybridization process such that desirable genes or characters are transmitted to their progenies. Combining ability can be partitioned into two components: variance due to general combining ability (GCA) and variance due to specific combining ability (SCA). General combining ability is defined as the average performance of a parent in hybrid combination and is recognized primarily as a measure of additive gene action whereas specific combining ability describes those cases in which certain hybrid combinations do relatively better or worse than what would be expected on the basis of the average performance of the parent, and is regarded as an estimate of non-additive gene action such as dominance and epistasis. The general combining ability information helps to estimate the suitability of a line as potential parent in hybrid development and as breeding material for genetic improvement of the desired trait, while specific combining ability estimate provides information about the performance of the hybrids. The difference in general combining ability among lines are mainly due to additive genetic effects and higher order additive interactions, while the difference in specific combining ability are primarily attributed to the non-additive dominance genetic effect.

Mating designs are used to estimate combining abilities of parental populations involved in making crosses and to determine the type of gene actions operating in the inheritance of the traits under investigation. In plant breeding, various mating designs and arrangements are used by breeders and geneticists to generate improved plants. Plant breeders need to quantify additive and non-additive components of genetic variance in order to determine appropriate selection methods to improve quantitative characteristics. Number of mating design is used for number of best producing progenies by breeders and geneticists in plant breeding programmed for their success and improvement to next generations. Mating designs were developed to study quantitative characters. Various mating designs were used by plant breeders and geneticist for improvement of plants. For getting success in plant breeding, the selection of good mating design and parents is necessary. Several factors affect the choice of mating designs such as the type of crossing to be used (Artificial or natural), type of pollination (Self or cross pollinated), type of pollen dissemination (Insect or wind), the purpose of project (For genetic or breeding studies), the presence of male sterility system and the size of population required.

Generally, selection of suitable parents and good mating designs are keys to the successful of plant breeding schemes. Number of mating designs were used to estimate genetic diversity for crop improvement, like as path coefficient analysis, diallel mating design, line ×tester, generation mean analysis, bi-parental cross, stability

analysis, heritability and genetic advance, combing ability, heterosis and inbreeding depression, gene action in plant breeding, triple test cross analysis and correlation in plant breeding population. The choice of a mating design for estimating genetic variances should be dictated by the objectives of the study, time, space, cost and other biological limitations. The population genetic variance can be described in terms of GCA and SCA variances which could further be partitioned into additive and non-additive components of variation.

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